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Resource and niche differentiation mechanisms by sympatric Early Pleistocene ungulates: the case study of Coste San Giacomo

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ABSTRACT

Resource competition and niche partitioning among the exceptionally high number of sympatric ungulates of the Early Pleistocene site of Coste San Giacomo (Central Italy) is here examined through the study of their dietary proclivities and body size. The main aim of this study is to investigate the niche differentiation mechanisms that let the fossil ungulates coexist in the same region. We also provide information about the complementarity of two different methodologies that observe diet variation at a different time scales (inner and outer mesowear) in the study of dental wear patterns of fossil ungulates. Results from analyses of dental wear degree and body masses predictions show that a wide range of feeding behaviours were adopted by the taxonomical groups (i.e., cervids, bovids and equids) in order to avoid competition. Among larger ungulates diet ranges from strict browsing (*Eucladoceros* sp., *Gazellospira torticornis*), to mixed feeding (*Gallogoral meneghinii*, *Leptobos* sp.) to pure grazing (*Equus stenonis*), whereas smaller taxa are more selective feeders (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*) with only one exception (*Gazella borbonica*). When taxa with the same feeding behaviour occurred in the same habitat, competition was minimised by differences in body size.

1. Introduction

Competition between species occurs when species occupy the same habitat, use the same resources and when said resources are limiting. Ungulates can directly compete for shared resources of food or space, or can interfere against resources used by another species (interference competition) (Latham, 1999). Niche differentiation mechanisms, such as habitat segregation, differences in body weights and specialized dietary adaptations as well as beneficial interactions (facilitation), can however minimize competition allowing the co-existence of different sympatric ungulate in a region, (De Boer and Prins, 1990; Klein and Bay, 1994; Latham, 1999; Prins et al., 2006; Sietses et al., 2009). Such ecological mechanisms in fossil assemblages are often difficult to investigate, but they are indeed important to understand interspecific relationship among taxa, especially in those localities where multiple fossil ungulates occurred and overlapped. In extant herbivore ungulates, diet quality and body size are strongly related (Henley and Ward, 2006; Codron et al., 2007), with the former decreasing when body size increases (Mysterud, 1998; references within; Codron et al., 2007) and with animals of similar body mass and digestive system foraging on similar foods (Henley and Ward, 2006). This is because larger herbivores require larger quantities of food, and the more abundant plants parts (e.g. stems or twigs) are generally of lower nutritional quality than less abundant, higher-quality parts (e.g. leaves, fruits or forbs). Contrarily, smaller herbivores require smaller quantities of food, and they are generally selective feeders adapting to use mostly high quality forage (Clauss et al., 2013). As a result, herbivores exhibiting different body size and different dietary preferences can coexist in the same ecosystem (Prins and Olff,

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1998).

The Early Pleistocene large mammal assemblage of Coste San Giacomo (herein referred as CSG) in Anagni (Central Italy), recently dated around 2.1 Ma (Bellucci et al., 2014), is characterized by an unusual abundance of herbivore taxa, mostly represented by artiodactyls and perissodactyls (Bellucci et al., 2012; Strani et al., 2015). Among these, three fossil cervids (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus* and *Eucladoceros* sp.), four bovids (*Gallogoral meneghinii*, *Gazella borbonica*, *Gazellospira torticornis* and *Leptobos* sp.), and one equid (*Equus stenonis*) have been identified (Bellucci et al., 2012; Bellucci and Sardella, 2015). These taxa have been recently studied from a paleodietary point of view in order to gain new information about the palaeoclimate and palaeoenvironmental conditions that prevailed in Central Italy during the Gelasian (Early Pleistocene) through the analysis of their dental wear degree (mesowear) and molar crown height (hypsodonty) (Strani et al., 2015).

With this new updated information of their dietary preferences, this research relies on the working hypothesis that the extraordinary number of herbivore ungulates werw forced to exhibit different mechanisms in CSG in order to avoid strong direct competition, partition the niche space and optimize exploitation of the available vegetation. We consider indeed CSG as an exceptional case study to do this because of the wide spectrum of diets and body sizes exhibited, and the occurrence of different taxonomic groups in the same assemblage. To do so, we focus on new traits of ecological relevance (e.g., body size) and more precise dietary inferences also adopting the new inner mesowear approach (Solounias et al., 2014) to better understand how niche and resource partitioning work in fossil communities. Importantly, and given the abundant dietary data provided by the CSG mammal community, here we also aim to examine the complementary nature of two proxy methods based on the dental wear degree (inner and outer mesowear) comparing the obtained results and test their combined use in paleoecological studies.

2. Material and methods

The studied fossil material belongs to the Early Pleistocene (Gelasian) locality of Coste San Giacomo (CSG) near the town of Anagni (Frosinone, Central Italy). Extensive fieldwork has been carried out since 1978 by researchers of the Italian Institute of Human Palaeontology (IsIPU) (Segre Naldini et al., 2009; Bellucci et al., 2014 and references therein). The material is currently housed at the IsIPU laboratory in Anagni (Frosinone, Central Italy). The updated faunal list of CSG (Bellucci et al., 2014) comprises 19 large and 7 micromammal taxa. Among them, the fossil material here studied consists of 102 dental (molar) specimens of the following ungulate taxa: *Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*, *Eucladoceros* sp., *Gazella borbonica*, *Gazellospira torticornis*, *Gallogoral meneghinii*, *Leptobos* sp. and *Equus stenonis*.

2.1. Body mass estimation

Herbivore body mass is an important ecological trait in niche repartitioning as it influences diet choices (Henley and Ward, 2006). Mammalian body size is usually predicted by proximal limb bones (Scott, 1983, 1990), cranial (MacFadden and Hulbert, 1990) or dental (Janis, 1990) measurements. Due to the lack of well represented post-cranial and cranial remains for most of the CSG ungulates, only dental measurements were taken. The occlusal lengths of upper second (M2) or lower first (m1) molars were used to estimate body size following the procedure described by Janis (1990). The intercepts and slopes of prediction equations for the different cranio-dental measurements for 1) perissodactyls, 2) cervids only and 3) bovids only were taken from Janis (1990). That is, in order to predict the weight of the CSG taxa, we used the provided slopes and intercepts of the linear regressions based on log M2 and log m1 occlusal length, form the “Perissodactyls and hyracoids only” group (for *E. stenonis*), from the “Cervids only group” (for *Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*, *Eucladoceros* sp.), and from the “Bovids only group” (for *Gazella borbonica*, *Gazellospira torticornis* and *Gallogoral meneghinii*). The inverse logarithm was calculated to obtain the body mass for each animal.

The results were compared with modern taxa listed in Janis (1990). Note that body size estimation for *Leptobos* sp. was not performed due to the lack of both M2 and m1 specimens for this taxon.

2.2. Dental mesowear

Mesowear is considered a good dietary indicator in herbivore species, as it represents the cumulative effects of the items ingested (both foods and exogenous particles such as dust and grit) on the dental morphology that are produced in a long period of time compared to the lifespan of the animal (Fortelius and Solounias, 2000).

Traditional mesowear (Fortelius and Solounias, 2000), referred as “outer mesowear” (Solounias et al., 2014; Danowitz et al., 2016), analyses the sharpness (i.e., morphology) of the cusps and the height of the occlusal relief of the most labial enamel bands of upper molars and the most lingual of the lower ones (Kaiser and Solounias, 2003; DeMiguel et al., 2012). In Strani et al. (2015), occlusal relief (high or low) and cusp shape (sharp, rounded or blunt) of the apex of the paracone and metacone of the M1-M3 and the metaconid and entoconid of the m1−m3 were examined and scored, and data compared with those of a database of extant ungulates with known diets (Fortelius and Solounias, 2000). The variables were also converted to a score following Rivals et al. (2009) as follows: (0) teeth showing a combination of high relief and sharp cusps; (1) teeth with high relief and rounded cusps; (2) teeth with low relief and rounded cusps; (2.5) teeth with low relief and sharp cusps; and (3) teeth with low relief and blunt cusps.

The inner mesowear method, recently developed by Solounias et al. (2014), analyses instead the second enamel band that forms the lingual margin of the metacone or paracone from an occlusal view, which is generally more frequently preserved in fossil specimens. Inner mesowear reflects dietary preferences that are intermediate in time (days-weeks; Danowitz et al., 2016) between outer mesowear (months-years; Fortelius and Solounias, 2000; Mihlbachler et al., 2011; Sánchez-Hernández et al., 2016) and dental microwear (days-hours; Solounias and Semprebon, 2002). For inner mesowear, the enamel band is scored on the mesial and distal sides of the metacone using a 4 point scaling system described by Solounias et al. (2014) and Danowitz et al. (2016): (1) flat and planar with no gouges or indentations on the surface of the enamel; (2) nearly flat with several gouges that traverse the surface from either edge—the labial and lingual edges of the enamel band are somewhat rounded; (3) similar to score 2, but more rounded with less defined edges and more gouges; and (4) rounded—the surface is smooth without gouges, and there are no well-defined edges. The junction of the mesial and distal sides termed J is similarly scored: (1) it joins at a sharp, well-defined junction; (2) it is somewhat sharp, and often contains a gouge; (3) it is rounded, but the mesial and distal sides appear as distinct, separate surfaces; and (4) the J point lacks a discrete apex, and the mesial and distal sides of the enamel band form one continuous surface. The method was originally applied by Solounias et al. (2014) only on upper second molars (M2), and here it has been extended to M1 and M3 molars of different individuals in order to widen the sample and

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allow for more complete comparisons among mesowear databases (Table 1). Whenever possible, we used the enamel band of the metacone of the upper molars. If this region was taphonomically damaged, the band of the paracone was examined. We compared our results of the average inner mesowear scores of the mesial, J point and distal surfaces with those of a comprehensive database (Danowitz et al., 2016) of 8 extant ungulates with well-studied diets (browsing, mixed feeding and grazing).

2.3. Statistical methods

Discriminant analyses were performed to analyse the resolution of both outer and inner mesowear variables applied to the fossil taxa. For the outer mesowear, the percentage of high relief, rounded and blunt cusps were used as independent variables and two dietary (conservative and radical; Fortelius and Solounias, 2000) classifications were used alternately as a grouping variable in order to recognize those taxa that although showing mixed-feeders adaptations had diets engaged in either browse or grass consumption. For the inner mesowear, we used the diet of extant species (Danowitz et al., 2016) as a grouping variable, and the mesial, distal and J point scores as variables to infer the dietary preferences of species. All analyses were performed using SPSS Statistics 23.

3. Results

3.1. Body mass estimation

For the cervids, the body mass has been estimated around 84 kg for *Axis* cf. *lyra* (comparable to the extant mule deer *Odocoileus hemionus*; 91/57 kg; Janis, 1990), 63 kg for *Croizetoceros* cf. *ramosus* (similar to that of the modern sika deer *Cervus nippon* [64/41 kg; (Janis, 1990)] and the fallow deer *Dama dama* [67/44 kg; (Janis, 1990)], and around 239 kg for *Eucladoceros* sp. (comparable to the wapiti *Cervus canadensis*; 400/250 kg; Janis, 1990). With regard to the bovids, the body mass of *Gallogoral meneghinii* is around 217 kg (comparable to the extant takin *Budorcas taxicolor*; 250 kg; Janis, 1990), 30 kg for *Gazella borbonica* (similar to the dibatag *Ammodorcas clarkei*) and 214 kg for *Gazellospira torticornis* (comparable to the mountain nyala *Tragelaphus buxtoni*; 216/150 kg; Janis, 1990). Finally, the body mass of the equid *Equus stenonis* is around 386 kg (thus being similar to that of the Grévy's zebra *Equus grevyi*; 400 kg; Janis, 1990).

3.2. Outer (traditional) mesowear

Analyses of outer mesowear of ungulates from CSG (Strani et al., 2015) show different patterns of wear and a wide spectrum of feeding behaviours, with cervids (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus* and *Eucladoceros* sp.) and the bovid *G. torticornis* having a predominance of sharp cusps and high occlusal relief and browser diets; the bovids *G. borbonica*, *G. meneghinii* and *Leptobos* sp. showing sharp and rounded cusps and high relief and intermediate diets; and the equid *E. stenonis* showing blunt and rounded cusps and low relief and a strict grazer behaviour (Table 1).

3.3. Inner mesowear

The distribution of the inner mesowear scores (mesial, J point and distal) of the ungulate community of CSG includes mostly intermediate values (from 1 to 3) (Table 2). The highest ones (>3) are observed in *E. stenonis*. When plotting data from CSG with those of modern ungulates grouped into browsers, mixed feeders and grazers (Fig. 1), the scores distribution suggests a spectrum of dietary preferences that extend from browsing to mixed feeding, with the exception of *E. stenonis*. The scores of *A.* cf. *lyra*, *C.* cf. *ramosus*, *Eucladoceros* sp., and *G. torticornis* are comparable to those of modern browsers and a high variability of the mesial and distal scores are observed (though the J point score tends to have similar values). *G. meneghinii* scores are similar to those of a browser as well, while higher scores are observed in *Leptobos* sp. and *G. borbonica* which are placed close to mixed feeders. These results should however be taken as tentative due to the small sample available for these taxa ($N = 2$). *E. stenonis* differs by being the only species whose average inner mesowear scores are comparable to those of modern grazers.

3.4. Discriminant analyses

Discriminant analysis performed with the outer mesowear variables provides a satisfactory dietary discrimination with 74.1% of extant taxa (68.5% in cross-validation, $p < 0.001$ for Function 1, and $p = 0.38$ for Function 2 with canonical correlation of 0.80 and 0.35) correctly classified according to a conservative classification and 74.1% (74.1% in cross-validation, $p < 0.001$ for Function 1, and $p = 0.50$ for Function 2 with canonical correlation of 0.80 and 0.16) according to the radical one. Bivariate diagrams based on the discriminant analysis (Fig. 2A–B) show that all the fossil deer and the antelope *G. torticornis* are classified as browser, *G. meneghinii*, *G. borbonica* as mixed feeders, and *E. stenonis* as a grazer in both the conservative (Fig. 2A) and radical (Fig. 2B) classifications. *Leptobos* sp. is classified as a mixed feeder in the conservative classification (Fig. 2A), and considered as a grazer in the radical (Fig. 2B).

Discriminant analyses for the inner mesowear predicted the diet of the individuals with a high accuracy rate (73,6% of cases correctly classified; 71,3% in cross-validation) resulted in two significant discriminant functions ($p < 0.001$ for Function 1, and $p = 0.74$ for Function 2) with canonical correlation of 0.80 and 0.08. Note that

Table 1
Summary of body mass estimation, outer and inner mesowear. Abbreviations: Number of specimens (N); size estimation based on M2 (M2 L), m1 (m1 L) length and average size (AS); percentage of specimens with high (%H) and low (%L) occlusal relief; percentage of specimens with sharp (%S), rounded (%R) and blunt (%B) cusps; Mesowear Score (MS); mesial (Mesial), distal (Distal) and J point (J) scores; and diet classification (Diet). Outer mesowear data from Strani et al. (2015).

Species	Body Mass (kg)			Outer Mesowear							Inner Mesowear			
	M2 L (N)	M1 L (N)	AS	N	%H	%L	%S	%R	%B	MS	N	Mesial	Distal	J
Axis cf. *lyra*	75.87 (2)	92.89 (5)	84.38	26	100	0	76.9	23.1	0	0.19	7	1.5	1.8	1.43
Croizetoceros cf. *ramosus*	/	63.39 (1)	63.39	5	100	0	80	20	0	0.2	3	1	1.5	1.67
Eucladoceros sp.	214.70 (3)	263.13 (1)	239.9	26	100	0	88.5	11.5	0	0.12	12	1.3	1.5	1.83
Gazella borbonica	31.08 (1)	28.74 (3)	29.91	8	87.5	12.5	50	50	0	0.63	2	2.5	2.5	3
Gazellospira torticornis	214.44 (4)	/	214.4	8	100	0	87.5	12.5	0	0.13	4	1.5	1	1.75
Gallogoral meneghini	217.27 (1)	/	217.3	2	100	0	50	50	0	0.5	2	1.5	1	2
Leptobos sp.	/	/	/	2	100	0	0	100	0	1	2	2.5	2.5	2.5
Equus stenoni	303.17 (5)	468.77 (4)	387	21	4.8	95.2	28.6	38.1	28.6	2.33	11	3.33	3.29	3.63

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Table 2
Dietary predictions from discriminant analysis using inner mesowear variables.

Species	Frequency Browser	Frequency Mixed Feeder	Frequency Grazer	Undetermined
Axis cf. *lyra*	4			3
Croizetoceros cf. *ramosu*	2			1
Eucladoceros sp.	8			4
Gazella borbonica		2		
Gazellospira torticornis	2			
Gallogoral meneghinii	1			1
Leptobos sp.	1	1		
Equus stenonis		1	5	5

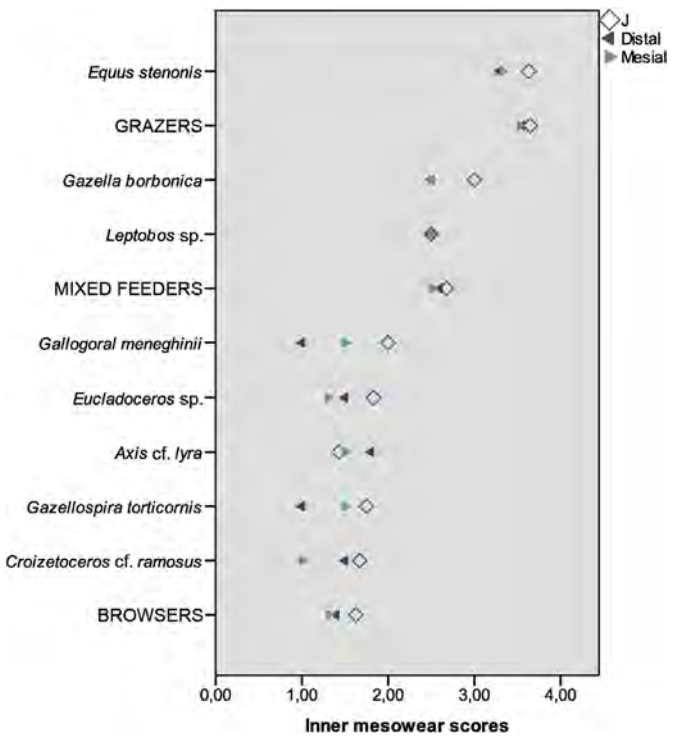

Fig. 1. Mean inner mesowear scores for fossil taxa and modern browsers, mixed feeders and grazers (data for extant species from Danowitz et al., 2016).

individuals lacking mesial/distal bands or J scores were not classified (Undetermined). Table 2 depicts individual results of the dental specimens and their variability thus showing that all the suitable individuals of *Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*, *Eucladoceros* sp., *Gazellospira torticornis* and *Gallogoral meneghinii* are browsers, *Gazella borbonica* individuals are mixed feeders, one specimen of *Leptobos* sp. is considered to be a browser and other a mixed feeder, and most of the individuals of *E. stenonis* are grazers (with only one classified as a mixed feeder).

Globally, inner mesowear results (Table 3) considering both the individual results (Table 2) and the mean distribution of the inner mesowear scores (Fig. 1) show a diversity of dietary preferences. A browsing feeding behaviour can be observed for the cervids as well as for the bovids *G. torticornis* and *G. meneghinii*. Results also indicate a mixed feeding behaviour for *G. borbonica* and *Leptobos* sp., whereas *E. stenonis* appears to be a grazer.

4. Discussion

4.1. Comparison between outer and inner mesowear

Both outer and inner mesowear methods show similar dietary predictions for most of the cases (Table 3), and only one discrepancy can be observed according to the primary (conservative classification) diet of the species. Thus, *G. meneghinii* is classified as a mixed feeder and a browser according to the outer and inner mesowear, respectively. Given that the inner mesowear occurs at a smaller time scale than the outer, this can indicate a mixed feeding-towards-browsing diet type or a temporary shift towards a more browsing feeding behaviour. When the secondary (or more radical)

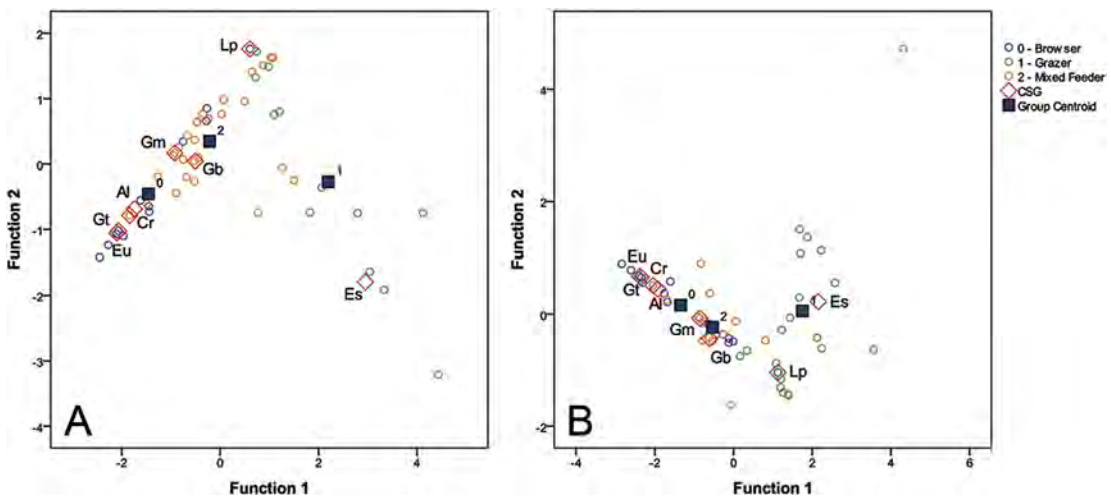

Fig. 2. Bivariate diagrams based on discriminant analysis using conservative (A) and radical (B) classifications. Fossil taxa abbreviations: Al, *Axis* cf. *lyra*; Cr, *Croizetoceros* cf. *ramosus*; Eu, *Eucladoceros* sp.; Gb, *Gazella borbonica*; Gt, *Gazellospira torticornis*; Gm, *Gallogoral meneghinii*; Lp, *Leptobos* sp.; Es, *Equus stenonis* (data from Strani et al., 2015).

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Table 3
Dietary inference from outer and inner mesowear analyses.

Species	Outer mesowear		Inner mesowear
	Diet prediction (conservative classification)	Diet prediction (radical classification)	Diet prediction
Axis cf. *lyra*	Browser	Browser	Browser
Croizetoceros cf. *ramosus*	Browser	Browser	Browser
Eucladoceros sp.	Browser	Browser	Browser
Gazella borbonica	Mixed Feeder	Mixed Feeder	Mixed Feeder
Gazellospira torticornis	Browser	Browser	Browser
Gallogoral meneghinii	Mixed Feeder	Mixed Feeder	Browser
Leptobos sp.	Mixed Feeder	Grazer	Mixed Feeder
Equus stenonis	Grazer	Grazer	Grazer

diet obtained from the outer mesowear is compared with results from the inner mesowear, there is a discrepancy for *Leptobos* sp. Inner mesowear scores indicate a mixed feeding behaviour (Table 3, Fig. 1) thus differing from the grazing diet inferred from the radical classification (Table 3, Fig. 2A–B). This discrepancy may suggest that this taxon leaned generally towards a diet richer in abrasive foods (months-to-years according to the outer mesowear time scale), and that it assumed a more mixed feeding behaviour during short periods of time (days-to-weeks inner mesowear time scale). The small available samples for both these taxa may impact the robusticity of these interpretations, but it must be noted that the discrepancies were obtained between the mixed feeder and the browser/grazer style and, importantly, no species were classified as a grazer while being a browser, and vice versa.

Overall, both methods are here shown to provide very similar (almost identical) results, and it should be noted that the inner mesowear is most effective with specimens where all the three variables can be scored (when all the three parts of the inner second enamel band are not damaged or ruined), as highlighted by the number of undetermined individuals (Table 2). Nevertheless using both methods is highly advantageous and recommendable to obtain information about diet variation at different time scales.

4.2. Niche and resource partitioning

All the cervids (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus* and *Eucladoceros* sp.) share similar dental wear pattern to those of extant browsers. However, the size of the two former differs greatly from that of *Eucladoceros* sp. by being significantly smaller (84 and 63 kg vs. 239 kg, respectively). It is therefore possible that, despite exhibiting the same type of diet, differences in foraging in terms of height (vertical stratification) and the incorporation of different browse and ligneous foods, may explain the coexistence of the two small deer with *Eucladoceros* sp. Thus, *Eucladoceros* due to its larger body size may have exhibited a generally poorer quality diet (such as twigs of ligneous plants) if compared to that of the other cervids, and this could have been more evident during (short) periods of drier conditions and resource limitation. In this adverse periods small browsers would have foraged on most of the scarce high quality foods (see Prins et al., 2006 for an explanation of modern African species). Alcalde (2013) reports post-cranial adaptations for *Axis lyra* (=*Metacervoceros rhenanus*) similar to those of some modern browser species (such as the Eurasian elk *Alces alces*) that dwell and feed on humid areas. Although *A. alces* is significantly larger than all the CSG deer (450/318 kg; Janis, 1990), it has outer and inner mesowear comparable to those of *Axis* cf. *lyra*. Both species display high percentage of sharp cusps coupled with mesial, distal and J scores close to 1.5 (Table 2) (Fortelius and Solounias, 2000; Solounias et al., 2014; Danowitz et al., 2016). This suggests that CSG *Axis* cf. *lyra* may had preferably browsed in wetlands areas. *G. torticornis* is the other taxon whose wear patterns reflect a selective (browsing) feeding behaviour and is comparable in size to *Eucladoceros* sp. (Fig. 3). Because post-cranial morphologies similar to those of modern gazelles have been reported for this fossil antelope (Alcalde, 2013), an adaptation to arid habitats as well as some features typical of woodlands may have been possible. Thus, *G. torticornis* might have avoided competition with both the medium-sized browser deer *Eucladoceros* sp. and larger open-land taxa such as the mixed feeders *Leptobos* sp. and *G. meneghinii* by browsing on brushes of transitional ecotones (e.g., transition zone between closed woodland and open grassland) or by partitioning the available vegetation in terms of height above ground level (Hulbert and Andersen, 2001) foraging on the same plant species but eating different parts as observed in African Wildebeest and Zebra (Owaga, 1975).

Alcalde (2013) also reports post-cranial adaptations for steep terrains and rather open landscapes for *G. meneghinii*, thus habitat segregation (i.e. a preference for mountainous regions) combined with a more flexible diet may had been key factors for niche partitioning in *G. meneghinii* populations. Wear patterns for *G. borbonica* indicate a mixed feeding (with a probably tendency towards grazing) composed by a higher amount of abrasives in diet if compared to all the cervids and the other bovids from CSG. This seems to be related to an occurrence in more open grasslands habitats (Strani et al., 2015). *G. borbonica* is also the smallest ungulate of the mammal assemblage (Fig. 3) and its broader diet fits well with the coexistence with the other larger mixed feeders *Leptobos* sp. and *G. meneghinii* and the strict grazer *E. stenonis* in

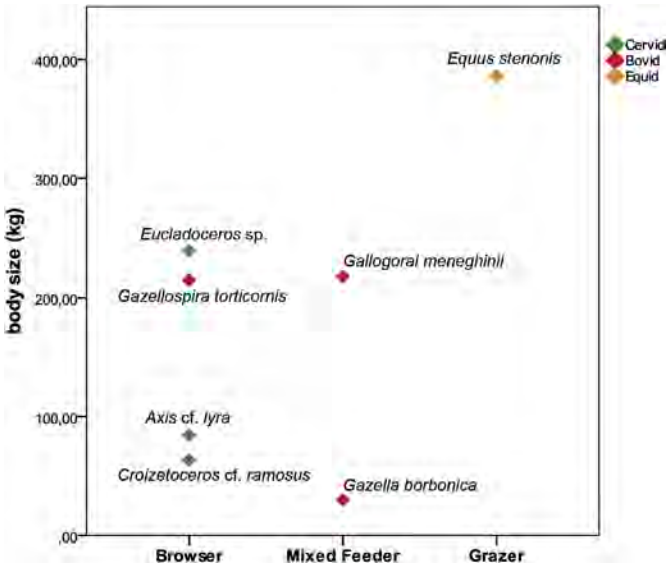

Fig. 3. Average body size (kg) of the CSG ungulates plotted against feeding behaviour.

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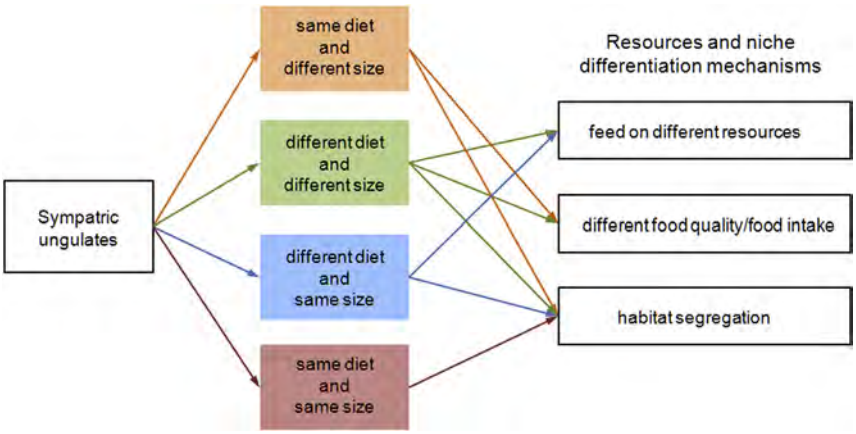

Fig. 4. Flow diagram showing niche partitioning mechanisms in sympatric ungulates based on dietary preferences and body size.

open environments. Overall, larger ungulates tend to display different diet ranging from strict browsing to grazing, whereas small taxa, with the exception of the bovid *G. borbonica*, appear to be more selective feeders (Fig. 3). It should also be noted that *A.* cf. *lyra*, *Eucladoceros* sp. and *E. stenonis* are the most common and well represented ungulates of the CSG assemblage (Bellucci et al., 2014), and the relative abundance of these species in the fossil deposit most probably influenced niche partitioning among the CSG herbivores as well. According to niche breadth concepts modern assemblage composed of abundant and relatively rare ungulates, uncommon species may persist by either consuming preferably few sparsely but widely available resource types, or by foraging in areas where their favoured resource is concentrated and aren't heavily exploited by the most common species (Brown, 1984; Macandza et al., 2012 and references therein). Following this it can be hypothesize that less common CSG ungulate taxa (*C.* cf *ramosus*, *G. torticornis*, *G. borbonica, Leptobos* sp., *G. meneghinii*) had a narrower niche breadth, restricting their diet to selected resources or smaller patches, while the most common species (*A.* cf. *lyra*, *Eucladoceros* sp., *E. stenonis*) would exploit a broader landscape.

According to all this, we propose a schematic model for explaining the major mechanisms of niche differentiation among sympatric herbivore ungulates based on diet and body masses (Fig. 4).

5. Conclusions

Data obtained from this study inform about how niche differentiation occurs in fossil assemblages, which is especially relevant in the study of species coexistence under limiting resources. Using the Early Pleistocene assemblage of Coste San Giacomo as a case study, we see that ungulates sharing the same feeding behaviour (browsing, mixed feeding, grazing) generally have different body size indicating different food intake demands and thus different diet quality. For similar-sized ungulates, a difference in the feeding behaviour is usually observed, and by consuming different type of resources they can share same habitats. For ungulates that share dietary type and body size, differences in habitat preference play a key role in niche partitioning with generalist species feeding in grasslands and woodlands (or in transitional areas), and more specialised taxa foraging mostly in specific environments (e.g., wetlands, rocky regions).

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